Canadian Science Publishing

ARTICLE

The response of a brown trout (*Salmo trutta*) population to reintroduced Eurasian beaver (*Castor fiber*) habitat modification

Robert J. Needham, Martin Gaywood, Angus Tree, Nick Sotherton, Dylan Roberts, Colin W. Bean, and Paul S. Kemp

Abstract: Globally, freshwaters are the most degraded and threatened of all ecosystems. In northern temperate regions, beaver (*Castor* spp.) reintroductions are increasingly used as a low-cost and self-sustaining means to restore river corridors. River modifications by beavers can increase availability of suitable habitat for fish, including salmonids. This study investigated the response of a population of brown trout (*Salmo trutta*) to reintroduced Eurasian beaver (*Castor fiber*) habitat modifications in northern Scotland. The field site comprised two streams entering a common loch; one modified by beavers, the other unaltered. Electrofishing and PIT telemetry surveys indicated abundance of post-young-of-the-year (post-YOY) trout was higher in the modified stream. Considering juvenile year groups (YOY and post-YOY) combined, abundance and density varied with year and season. In the modified stream, fork length and mass were greater, there was a greater variety of age classes, and mean growth was positive during all seasons. Beavers had profound effects on the local brown trout population that promoted higher abundances of larger size classes. This study provides important insight into the possible future effect of beavers on freshwater ecosystems.

Résumé : Les écosystèmes d'eau douce sont les écosystèmes les plus dégradés et menacés sur terre. Dans les régions nordiques tempérées, les réintroductions de castors (*Castor* spp.) sont de plus en plus utilisées comme moyen peu coûteux et autosuffisant de restauration de couloirs fluviaux. Les modifications des rivières par les castors peuvent accroître la disponibilité d'habitats convenables pour les poissons, dont les salmonidés. L'étude se penche sur la réaction d'une population de truites brunes (*Salmo trutta*) à des modifications de l'habitat par des castors eurasiens (*Castor fiber*) réintroduits dans le nord de l'Écosse. Le site d'étude compte deux cours d'eau qui se jettent dans le même loch, un étant modifié par les castors et l'autre étant intact. Des relevés à la pêche électrique et de détection télémétrique d'étiquettes passives intégrées (PIT) indiquent une plus grande abondance de truites juvéniles de plus d'un an dans le cours d'eau modifié que dans le cours d'eau intact. L'examen de juvéniles de différents groupes d'âge (jeunes de l'année et de plus d'un an) combinés révèle que l'abondance et la densité varient selon l'année et la saison. Dans le cours d'eau modifié, la longueur à la fourche et la masse des poissons sont plus grandes, la diversité des classes d'âge est plus importante et le taux de croissance moyen est positif durant toutes les saisons. Les castors ont de profonds effets sur la population locale de truites brunes qui favorisent une plus grande abondance des classes de tailles plus grandes. L'étude fournit d'importants renseignements sur l'effet futur possible des castors sur les écosystèmes d'eau douce. [Traduit par la Rédaction]

Introduction

European rivers have been modified by man for centuries for agriculture (e.g., irrigation) (Moss 2008), domestic and industrial water supply (Rotiroti et al. 2019), generation of mechanical and electrical energy (Brown et al. 2018), navigation (Zajicek and Wolter 2019), and flood defence (Best 2019). As a consequence, rivers have been constrained, straightened, channelised, and impounded, so disrupting longitudinal, lateral and vertical connectivity and natural hydrogeomorphological and biological processes (Brown et al. 2018; Mossa et al. 2020). Although these changes have improved and maintained human quality of life, they have had serious negative consequences on aquatic biodiversity (Brown et al. 2018; Wohl et al. 2005) and as a result, freshwaters represent one of the worlds most threatened ecosystems (Belletti et al. 2020; Reid et al. 2013; Darwall et al. 2011).

There are multiple legislative drivers to restore European rivers, such as the EU Biodiversity Strategy that aims to reconnect 25 000 km of rivers by 2030 (Belletti et al. 2020). This builds on the EU Water Framework Directive (European Union 2000) that sought to achieve good ecological status across member states (Acreman and Ferguson 2010). River restoration in Europe is costly, with estimates ranging from €2.2–31 million·km^{-2} (Theodoropoulos et al. 2020). Considering that future funding for the environment is likely to become increasingly challenged in an era of post COVID-19 economic recovery, there is likely to be greater interest in strategies that enable targets to be achieved using low-cost "Nature Based Solutions" to re-establish processes rather than by adopting more traditional feature-based river restoration approaches that tend to be of limited value (Bernhardt and Palmer 2011).

Received 27 January 2021. Accepted 4 April 2021.

R.J. Needham and P.S. Kemp. International Centre for Ecohydraulics Research, University of Southampton, Southampton SO17 1BJ, UK.
M. Gaywood and A. Tree. NatureScot, Great Glen House, Leachkin Road, Inverness IV3 8NW, UK.
N. Sotherton and D. Roberts. Game and Wildlife Conservation Trust, Burgate Manor, Fordingbridge, Hampshire SP6 1EF, UK.
C.W. Bean. NatureScot, Clydebank Business Park, Clydebank G81 2NR, UK.
Corresponding author: Robert J. Needham (email: rjn1a13@soton.ac.uk).

Table 1. Perceived positive and negative effects of beaver activity on fish as identified by Kemp et al. (2012).

Positive effects	Negative effects
Heightened habitat availability–complexity	Barriers to fish movement
Improved overwintering habitat	Loss of spawning habitat
Enhanced rearing habitat	Altered temperature regime
Provision of cover	Reduced oxygen levels – habitat quality
Enhanced diversity–species richness	Altered flow regimes
Enriched abundance–productivity	Loss of cover
Provision of habitat under low flows	Reduced productivity
Provision of low flow refuge	Retarded fish growth
Establishment of temperature refuge	Abandonment of beaver settlements
Boosted water quality	Deterioration in water quality
Sediment trap	
Enriched invertebrate productivity	
Increased growth rates – fish condition	
Establishment of fishing areas	

As "Ecosystem Engineers", populations of Eurasian beavers (*Castor fiber*) provide a cost-efficient and self-sustaining means to restore rivers and streams by directly or indirectly controlling the availability of resources through habitat modification (Jones et al. 1994, 1997; Wright et al. 2002; Müller-Schwarze 2011). By increasing structural complexity, beavers facilitate the regeneration of processes that enable rivers and stream to function more naturally (Brown et al. 2018). As a result of this capacity to restore ecosystem function, habitat dynamics and heterogeneity, coupled with a public and associated political desire to restore a species extirpated by man, the reintroduction of beavers has gained increasing impetus in many European member states (Halley and Rosell 2002).

Beaver dams and their analogues accelerate the recovery of incised streams (Bouwes et al. 2016) and assist in the creation and maintenance of complex fluvial ecosystems (Pollock et al. 2014). As a result, beaver reintroductions are increasingly seen as an integral component of the wider restoration of river corridors (Bouwes et al. 2016; Burchsted et al. 2014). Beaver dams modify rivers and streams by impounding water, increasing the ratio of lentic to lotic habitat (Naimen et al. 1988), regulating flow (Pollock et al. 2003), and storing sediment and nutrients (Puttock et al. 2018). Furthermore, by building dams beavers reduce the density of riparian woodland, breaking up the canopy and enhancing light availability (Wright et al. 2002), increasing habitat diversity and flora richness (Smith and Mather 2013).

Despite the many documented ecological benefits of beaver activities, concerns remain regarding potential impacts of restored beaver populations on flooding of infrastructure and agricultural land, felling of commercial timber and ornamental trees (Campbell-Palmer et al. 2015), and the potential impacts on fish and fisheries, particularly those of economic importance such as salmonids (Kemp et al. 2012; Collen and Gibson 2000). By modifying riparian vegetation and providing in-stream structures, beaver dams can have both positive and negative effects on the production of stream dwelling salmonids (Kemp et al. 2012; Table 1). The relative magnitude of these impacts has been the subject of much debate and controversy (BSWG 2015).

Commonly cited benefits of beaver activity for salmonids include increased habitat heterogeneity (Hägglund and Sjöberg 1999; Smith and Mather 2013) and quality (Pollock et al. 2003). In particular, ponds created upstream of beaver dams provide juvenile overwintering and rearing habitat (Cunjak 1996) and critical refuge for larger fish (Hägglund and Sjöberg 1999). This results in increased fish abundance (Hägglund and Sjöberg 1999; Jakober et al. 1998), condition and growth (Sigourney et al. 2006; but see Rabe 1970, and Johnson et al. 1992), and overall productivity (Mitchell and Cunjak 2007; Nickelson et al. 1992; Pollock et al. 2004). Conversely, the principal negative consequence relates to the potential for dams to impede or delay salmonid migration, particularly for upstream moving adults during their migration along tributary streams to their spawning grounds (Malison and Halley 2020; Lokteff et al. 2013; Rupp 1955; Taylor et al. 2010). Furthermore, dams may reduce the availability of suitable spawning habitat in impounded areas, where flow velocity may be insufficient to purge the gravels of fine sediments that clog the interstices of gravels where the eggs and larval stages develop (Knudsen 1962; Taylor et al. 2010).

In considering the influence of beaver activity on fish, there is considerable research bias in favour of the North American beaver (*Castor canadensis*) (Kemp et al. 2012), while no studies have investigated the impact of *Castor fiber* on native salmonids in Great Britain. A lack of understanding of how beavers and fish interact in the British context threatens the development of robust management strategies that can, as a result, become unduly influenced by intuition, guesswork, and the perspectives and perceptions of stakeholder groups. This study investigated the response to beavers of a population of brown trout (*Salmo trutta*) inhabiting two streams that feed a common loch; one influenced by the construction of beaver dams (modified), the other unmodified (control). By comparing the response of fish occupying the two streams in which beaver dams were either present or absent, this study is the first conducted in Great Britain to shed light on the influence of beaver habitat modification on salmonids. In particular, attention focused on quantifying (1) trout abundance; (2) trout density; (3) fish size; (4) performance, quantified in terms of growth, taking into consideration inter-seasonal changes, and by comparing the results with model predictions for optimal growth of fish (Elliott et al. 1995); and (5) invertebrate community composition and abundance. We hypothesised that trout abundance (H1), density (H2) and size (fork length [FL], mm; and mass, g) (H3) would be higher in the beaver modified stream than in the control. We also predicted trout in the modified stream would exhibit positive growth performance (H4) and that invertebrate abundance (H5) would be higher in the modified stream than in the control. The results will help those tasked with managing freshwater systems where Eurasian beaver and brown trout coexist.

Methods

Study site

The Allt Coire an t- Seilich (modified) and Allt a' Choilich (control) are two first-order streams that flow in a northeast direction before entering an impounded loch, known locally as Loch Grant (17 644 m^2; 57.432°N, 4.424°W; ~160 m.a.s.l; Fig. 1). The loch

Fig. 1. Study site in which the response of a population of brown trout to fluvial landscape modification by beaver was investigated. The map illustrates the study area post-beaver modification, the Control as of July 2016 and the surrounding landscape and habitat types. Inset maps illustrate: (A) modified reaches, (B) stream depths within the modified area and (C) control reaches. The position of beaver dams, passive integrated transponder (PIT) loops (to monitor fish movement), and water data loggers (depth and temperature) are indicated. Map created using QGIS 2.18. Base map recreated from OS data © Crown Copyright (and database rights) 2020 OS 100025252. [Colour online.]

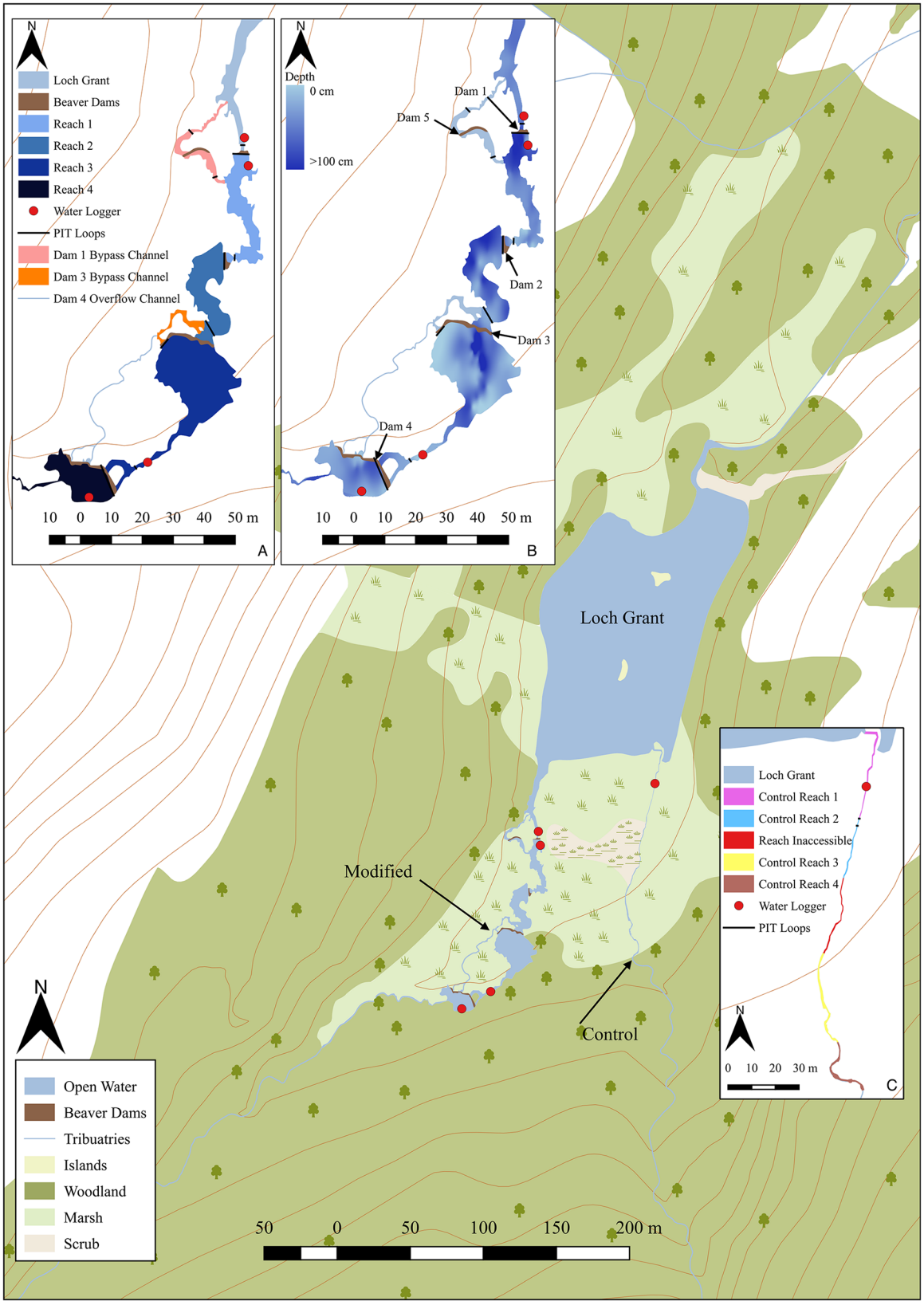


Table 2. Dimensions of dams (2015) constructed by Eurasian beaver released in 2008 on the Allt Coire an t- Seilich burn in Inverness-shire, Scotland.

Dam	Crest width (m)	Height (m)	Water depth downstream of dam (m)
1	5.1	0.56	0.47
2	5.8	0.57	0.26
3	19.3	0.55	0.13
4	24.0	0.97	0.19
5	10.1	0.54	0.13

outflow continues as the Allt a' Choilich, which flows northeast for 2 km before joining the Moniack Burn, which discharges directly into the Beauly Firth, Inverness-shire, Scotland.

The fish fauna is dominated by the freshwater-resident morphotype of brown trout, accompanied by three-spined stickleback (*Gasterosteus aculeatus*) and European eel (*Anguilla anguilla*). In 2008 a breeding pair of Eurasian beaver, of Bavarian origin, were released into the loch situated within a 40-ha enclosure, incorporating ~1.2 km of available stream habitat and ~0.6 km of loch shoreline.

Both modified and control streams exhibited similar physical, geomorphological and hydrological characteristics prior to beaver modification (C. Swift [landowner], personal communication, 2014). The modified stream was impounded in four locations by beaver dams to create four "modified" reaches (mean length 51.75 m) with an additional dam (Dam 5; Fig. 1; Table 2) constructed to the west of Dam 1 in 2016. The control site was similarly divided into four "control" reaches determined by riparian vegetation and accessibility (mean length 34.5 m) (Table A1) and remained unmodified by beavers during the study.

The four modified sections had a mean (±SD) wetted bank width of 5.82 m (±2.73 m), substrate that was dominated by silt, except immediately below dams where areas of gravel dominated, a predominant flow type classed as "deep pool", a mean velocity (±SD) of 0.09 $m \cdot s^{-1}$ (±0.07 $m \cdot s^{-1}$), and depths that regularly exceeded 0.5 m. The mean (±SD) wetted bank width for the control was 0.8 m (±0.26 m), the dominant substrate was pebble–cobble, the dominant flow type was classed as riffle, mean velocity (±SD) was 0.27 $m \cdot s^{-1}$ (±0.07 $m \cdot s^{-1}$), and depths did not exceed 0.2 m (Table A1).

Five water level loggers (OTT Orpheus Mini, OTT Hydromet) were installed in December 2014; one above and below Dams 1 and 4 and one in the control stream (Fig. 1). They recorded water depth and temperature every 5 min and averaged at 15 min intervals (Supplementary Fig. S1[1]).

The physical habitat characteristics of each reach were surveyed in May 2016, during spring baseflows, following the Scottish Fisheries Co-ordination Centre methodology (SFCC 2014) (Table A1). Coarse resolution mid-column velocity was recorded for each reach with an electromagnetic flow meter (0.001 $m \cdot s^{-1}$ resolution averaged over 60 s; Valeport Model 801, Valeport Ltd., UK). In July 2016, wetted width and bathymetry of the modified and control streams were quantified using differential GPS (Leica Viva GS14 Smart Antenna and a Viva CS15 Controller) (Fig. 1).

Fish surveys and PIT telemetry

Electrofishing surveys were conducted using a pulsed DC field (Easyfisher EFU – 1, 2.5A maximum output, 50/100 Hz) in the modified and control streams on six separate occasions during autumn (2014, 2015 and 2016), spring (2015 and 2016) and summer (2016) (Supplementary Table S1[1]). Captured fish were held in fresh aerated loch water for a maximum of 1 h prior to being anaesthetized using 2-Phenoxyethanol (concentration; 0.2 $mL \cdot L^{-1}$). FL (mm) and mass (g) were measured (Supplementary Table S1[1]), and trout longer than 65 mm were tagged with either half (HDX) or full duplex (FDX) passive integrated transponder (PIT) tags via ventral incision into the body cavity (65–80 mm FL = 8.4 mm FDX, n = 194, Biomark FDX-B Mini HPT8, Biomark, Idaho; 80–180 mm FL = 12 mm HDX, n = 581, Oregon RFID, Portland, Oregon; >180 mm FL = 23 mm HDX, n = 146, Oregon RFID, Portland, Oregon). Tagged fish were allowed to recover for at least 1 h and condition was visually assessed prior to release. To assess the impact of tagging on survival and to quantify tag retention, a sample of trout (n = 16, mean FL ± SD = 192.8 ± 72.1 mm in 2014; n = 28, mean FL ± SD = 171.9 ± 97.1 mm in 2015; and n = 30, mean FL ± SD = 109.4 ± 19.7 mm in 2016) were retained post-tagging for 48 hours in in-stream containers with through-flowing water. Tagged fish showed 100% tag retention (n = 74) and no mortality was observed. All fish were returned to the stream reach from where they were captured.

Invertebrate sampling

Invertebrate samples were collected from the modified and control streams in October 2016 at 10 m intervals providing 23 samples from each stream. Kick sampling (professional hand net [width — 250 mm, depth — 300 mm, mesh size — 1 mm]) methods were used where bed sediments were agitated for one minute directly upstream of the net. Samples were preserved on site in 100% ethanol before being diluted to a 70% solution for storage. In the laboratory, samples were identified to family (excluding Oligochaeta, which were identified to Order) and counted.

Ethics approval

Field work was performed after review and approval by the University of Southampton's Animal Welfare and Ethical Review Body (AWERB) following the 3R's ethical framework. Tagging was conducted in compliance with UK Home Office regulations under the *Animals (Scientific Procedures) Act* 1986 (project licence PPL 30/3196; personal licence PIL ID71D59A5).

Analysis

All data was tested for normality using Shapiro–Wilk's normality test, and homogeneity of variances assessed using a Levene's test. In instances where assumptions of normality failed, attempts to transform data were carried out and where this was not possible appropriate nonparametric tests were used. Despite deviations from normality in the 2015 density data and homogeneity of variance in 2016 density data, two-way ANOVAs were used as they are considered robust to slight deviations from normality and heterogeneity of variance when sample size is equal (Jaccard 1998).

Trout abundance and density

The terms *trout abundance* and *trout density* are used to differentiate between metrics that account for reach length and surface area, respectively. This accommodates the impounding effect of dams encountered in the modified reaches, but not the control. Trout abundance ($trout \cdot m^{-1}$) for each electrofishing reach was calculated as the quotient of the number of fish captured and reach length (m) measured along the central line of the channel. Reach values were aggregated to provide a mean for both the modified and control streams for each season. As seasonal data varied between years (Supplementary Table S1[1]), years were analysed independently. Analyses were performed twice for each year; first with all age classes included (YOY + post-YOY), and second, with young-of-the-year (YOY) fry (≤30 mm) and parr

[1]Supplementary data are available with the article at https://doi.org/10.1139/cjfas-2021-0023.

(31–60 mm) removed to control for seasonal influxes of YOY. Welch's two sample *t* tests compared the difference in abundance between the modified and control streams in autumn 2014. Two-way ANOVAs compared the effect of modified and control streams and season in 2015 and 2016 on trout abundance (m^{-1}) and post hoc comparisons were performed using Bonferroni corrections.

Trout density (trout·m^{-2}) was calculated as the quotient of the number of trout captured and surface area (quantified using the GIS base map; Fig. 1) of each reach. The statistical analysis of trout densities followed the same approach as that for abundance.

Variations in fork length and mass

The length-frequency distributions of trout caught in the modified and control streams were compared for each season using the two-sample Kolmogorov–Smirnov test. Seasonal data from multiple years was pooled; spring (2015 and 2016), summer (2016) and autumn (2014, 2015 and 2016). A Kruskal–Wallis test compared FL between the modified and control streams for all seasons and years and post hoc analyses were conducted using Dunn's-test for multiple comparisons of independent samples.

As specific growth rates could not be compared due to low recapture rates in the control, a Mann–Whitney (*U*) test compared mass of YOY parr (FL: 30–60 mm) and post-YOY (FL: 61–121 mm) between modified and control streams with seasons and years combined. FL parameters set for post-YOY were based on the largest trout caught in the control outside of the spawning period, deemed to be resident. Correlation between mass and FL of trout captured in the modified stream was calculated using Spearman's rank correlation and a linear regression model fitted.

Performance: growth

Correlation between growth in mass and FL was calculated using Spearman's rank correlation and a linear regression model fitted.

Using recapture data (defined as ≥14 days between release and recapture), growth rates were calculated for trout inhabiting the modified stream during five different periods: (1) winter 2014–2015 (October–December 2014 – March–April 2015 [n = 16]), (2) spring–summer 2015 (March–April 2015 – October 2015 [n = 16]), (3) winter 2015–2016 (October 2015 – April–May 2016 [n = 12]), (4) spring 2016 (April–May 2016 – July 2016 [n = 58]), and (5) summer 2016 (July–October 2016 [n = 17]). Growth rates for trout caught in the control stream were not calculated due to insufficient recaptures (n = 2 in summer 2016). The mean daily water temperature was calculated as the mean of all values recorded over 24 h for each data logger. For the period between 30 October and 18 December 2014, linear regression analysis was used to estimate the water temperature from air temperature measured at a local meteorological station. There was a strong linear relationship between water temperature and air temperature ($F_{[1,711]}$ = 5874, $p < 0.001$, r^2 = 0.89), with 74% of predictions within 1.5 °C of the observed values. Mean specific growth rate (SGR, %·day^{-1}) for PIT tagged trout recaptured during electrofishing surveys was calculated as

$$G = \left[(\log_e W_2 - \log_e W_1)/t\right] \times 100$$

where W_1 and W_2 are the initial and final trout mass (g), and t is the number of days between recapture (i.e., the growth period). For each fish, G was compared to an estimate of optimal growth (G_{op}) using the model developed by Elliott et al. (1995):

$$G_{op} = c \cdot W_1^{-b}(T - T_{lim})/(T_M - T_{lim})$$

where T is the mean water temperature during the growth period, and T_M and T_{lim} respectively represent the temperatures at which growth is optimal (13.11 °C) and ceases (limit). T_{lim} is the lower or upper value at which growth rate is zero (T_L [3.56 °C] or T_U [19.48 °C]) depending on whether T is higher or lower than T_M (i.e., $T_{lim} = T_L$ if $T < T_M$ or $T_{lim} = T_U$ if $T > T_M$). The mass exponent b is the power transformation that produces linear growth with time (0.308), and c is the growth rate of a 1 g trout at optimal temperature (2.803). All values were obtained from table 1 in Elliott et al. (1995). This growth model assumes fish fed to satiation under laboratory conditions. Welch's one-way test was used to compare growth rates between seasons. Pairwise *t* tests with no assumption of equal variances determined differences between periods.

Invertebrate abundance and community composition

The influence of beaver modification on total invertebrate abundance was analysed using Welch's two sample *t* test for unequal variance, and effect size calculated using Cohen's *d*. To evaluate the difference of community structure between the modified and control streams the relative abundance of taxa at each site was analysed with nonmetric multidimensional scaling (NMDS), Bray–Curtis distance metrics on two axes with a maximum of 50 restarts. To test whether habitat influenced community structure, the proportion of sample variation attributable to habitat type was calculated using permutational analysis of variance (ANOVA) (Adonis). Analysis was run using the R package Vegan. Statistical analyses were conducted using R.

Results

Trout abundance

In autumn 2014, when considering all age groups, trout abundance did not differ between the control and modified streams. However, in support of H1, post-YOY abundance was greater in the modified stream (0.52 [SE = 0.13] trout·m^{-1}) than the control (0.09 [SE = 0.06] trout·m^{-1}) (t_6 = –2.93, p = 0.03).

In 2015, when all age groups were included, abundance was greater in the modified stream (0.77 [SE = 0.14] trout·m^{-1}) than the control (0.31 [SE = 0.09] trout m^{-1}) ($F_{[1,13]}$ = 10.73, p = 0.007) in line with H1. Abundance did not differ with season and there was no interaction. When considering post-YOY trout only, abundance was also greater in the beaver-modified stream (0.70 [SE = 0.12] trout·m^{-1}) than the control (0.17 [SE = 0.07] trout·m^{-1}) ($F_{[1,13]}$ = 20.02, $p < 0.001$) in line with H1, and higher in autumn (0.58 [SE = 0.15] trout·m^{-1}) than spring (0.29 [SE = 0.10] trout·m^{-1}) ($F_{[1,13]}$ = 6.26, p = 0.03). There was no interaction between stream and season.

During 2016, When YOY fish were excluded, beaver modification had a strong influence on abundance ($F_{[1,18]}$ = 61.175, $p < 0.001$), being greater in the modified stream (0.50 trout·m^{-1} [SE = 0.38]) than the control (0.08 trout·m^{-1} [SE = 0.38]) in line with H1, a difference of 0.42 trout·m^{-1} (95% CI [0.31 to 0.54], $p < 0.001$) (Fig. 2B). There was no effect of season and no interaction between stream and season. When considering all age groups mean abundance varied with season ($F_{[2,18]}$ = 5.13, p = 0.02), being greatest during spring (0.95 [SE = 0.14] trout·m^{-1}) and lowest during autumn (0.34 [SE = 0.14] trout·m^{-1}) (95% CI [0.07 to 1.15], p = 0.02). There was no difference between spring and summer (0.84 [SE = 0.14] trout·m^{-1}) (95% CI [–0.43 to 0.65], p = 1.00) and between summer and autumn (95% CI [–0.04 to 1.04], p = 0.07) (Fig. 2A). There was no interaction between stream and season.

Trout density (m^{-2})

In autumn 2014, trout density did not differ between the modified and controls streams when all age groups were considered and when YOY were removed. This is in contradiction to H2.

During 2015, the densities were higher in the control (0.41 [SE = 0.13] trout·m^{-2}) than the modified stream (0.13 [SE = 0.03] trout·m^{-2}) ($F_{[1,13]}$ = 4.67, p = 0.05), when all age classes were considered in contradiction to H2. Density did not differ with season and there was no interaction. When YOY were excluded, density did not differ between the streams and there was no interaction. However, densities were higher in the autumn in both the modified (0.15 [SE =

Fig. 2. Mean ± SD brown trout abundance (trout·m^{-1}) during spring (black), summer (grey) and autumn (white) 2016 in the beaver-modified and control streams with all size class of trout included (A) and (B) fry ≤ 30 mm and parr 31–60 mm omitted.

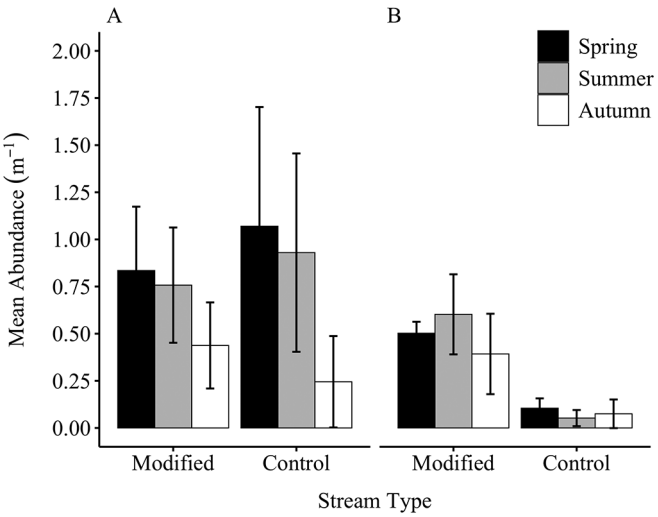
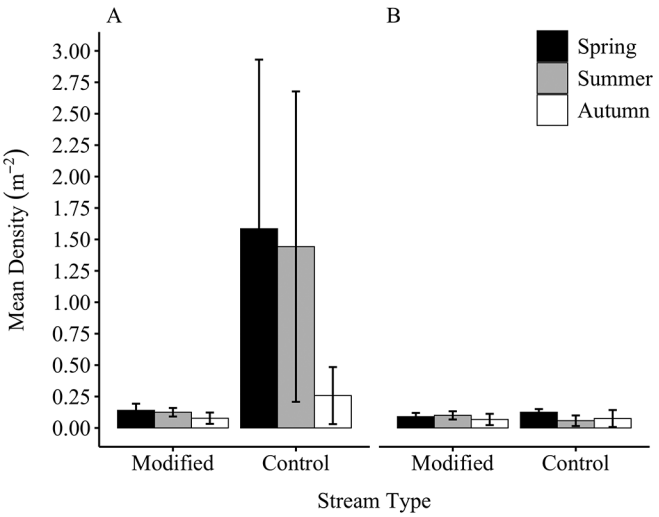


Fig. 3. Mean ± SD brown trout density (m^{-2}) during spring (black), summer (grey) and autumn (white) 2016 in the modified and control streams with all size class of trout included (A) and fry ≤ 30 mm and parr 31–60 mm omitted (B).



0.04] trout·m^{-2}) and control (0.38 [SE = 0.15] trout·m^{-2}) streams, compared to the spring (0.09 [SE = 0.02] and 0.07 [SE = 0.07] trout·m^{-2}, respectively) ($F_{[1,13]} = 4.75$, $p = 0.05$).

In 2016, densities were higher in the control (1.10 [SE = 0.22] trout·m^{-2}) than the modified stream (0.11 [SE = 0.22] trout·m^{-2}) ($F_{[1,18]} = 10.21$, $p = 0.005$) (Fig. 3A) in contradiction to H2. Season had no effect and there was no interaction between stream and season. When YOY were excluded, there was no influence of stream or season and no interaction (Fig. 3B).

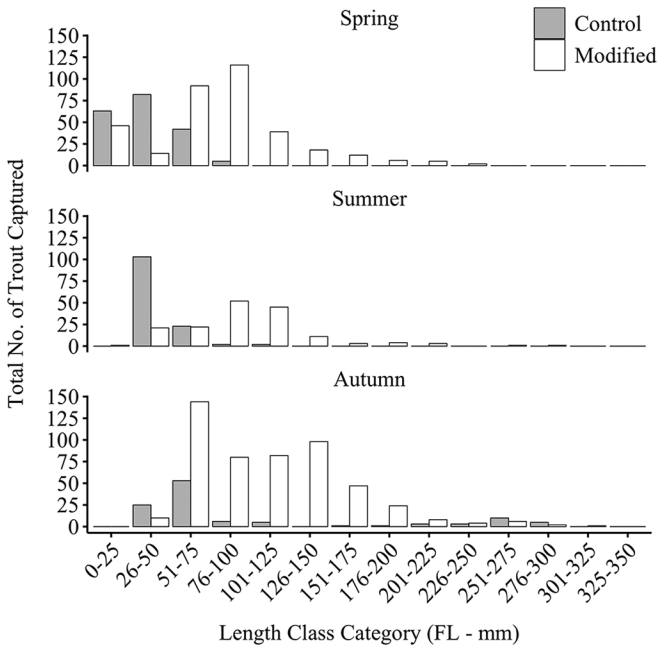
Fork length and mass

The distribution of length class frequency differed between the modified and control streams in spring ($D_{512} = 7.47$, $p < 0.01$), summer ($D_{294} = 6.37$, $p < 0.01$), and autumn ($D_{618} = 4.07$, $p < 0.01$) with a greater variety of size classes observed in the beaver modified stream during all seasons (Fig. 4). In spring, 77.5% of trout caught in the modified stream were ≥61 mm compared to 11.5% in the control, in summer 79.9% compared to 5.4%, and in autumn 91.5% compared to 49.1%.

In support of H3, fork length differed between trout captured in the modified and control streams ($\chi^2_{11} = 698.6$, $p < 0.01$; Fig. 5), with fish from the modified stream being longer in autumn 2014 (median = 116 mm, range = 56–314 mm, $p < 0.01$) and autumn 2016 (median = 114 mm, range = 42–215 mm, $p < 0.01$), but not in autumn 2015 ($p > 0.05$). The longest trout were found in the modified stream during spring 2015 (median = 86 mm, range = 55–221 mm, $p < 0.01$), spring 2016 (median = 74 mm, range = 23–202 mm, $p < 0.01$) and summer 2016 (median = 95.5 mm, range = 25–297 mm, $p < 0.01$). There was no difference in FL of trout captured in the modified stream among the three autumn periods. Similarly, the FL of trout captured in the control did not differ between autumn 2014 (median = 55 mm, range = 44–80 mm), and 2016 (median = 54 mm, range = 42–114 mm), but they were longer in autumn 2015 (median = 121 mm, range = 41–300 mm, $p < 0.01$). Trout FL was lowest in spring 2016 in both the modified ($n = 175$) (median = 74 mm, range = 23–202 mm, $p < 0.01$) and control streams (median = 26 mm, range = 22–95 mm, $p < 0.01$).

Mass of post-YOY trout ($U = 10996$, $r = -0.55$, $p < 0.001$) and YOY parr ($U = 5738.5$, $r = -0.68$, $p < 0.001$) differed between the modified and control streams, with heavier fish found in the modified stream (post-YOY: median 7.0 g [$n = 567$], YOY parr, median = 1.7 g

Fig. 4. The distribution of length class frequency between the beaver-modified and control streams in spring (2015 and 2016), summer (2016) and autumn (2014, 2015 and 2016). Seasonal data has been pooled for the years.



[$n = 86$]) than the control (post-YOY median 4.0 g [$n = 61$], YOY parr: median = 1.28 g [$n = 201$]) in line with H3 (Figs. 6A and 6B).

Performance: growth

Focusing on the modified stream only, there was a strong positive relationship between growth measured in terms of mass (g) and FL (mm) (correlation: $r_s = 0.816$, $p < 0.001$; linear regression model: $R^2 = 0.443$, $F_{[1,117]} = 92.86$, $p < 0.001$; Fig. 7).

Growth rates in mass (g) varied with season ($F_{[4,114]} = 26.004$, $p = <0.001$), with positive mean growth exhibited during all sampling periods in line with H4 (winter 2014–2015, mean ± SD =

Fig. 5. Fork length of trout captured in the modified "Mod" (clear boxes) and control "Con" (grey boxes) streams during autumn, spring and summer 2014, 2015 and 2016. The box plots illustrate the median (horizontal line), interquartile range (boxes) and overall range up to 1.5 times the interquartile range (whiskers). All outliers are depicted (clear circles).

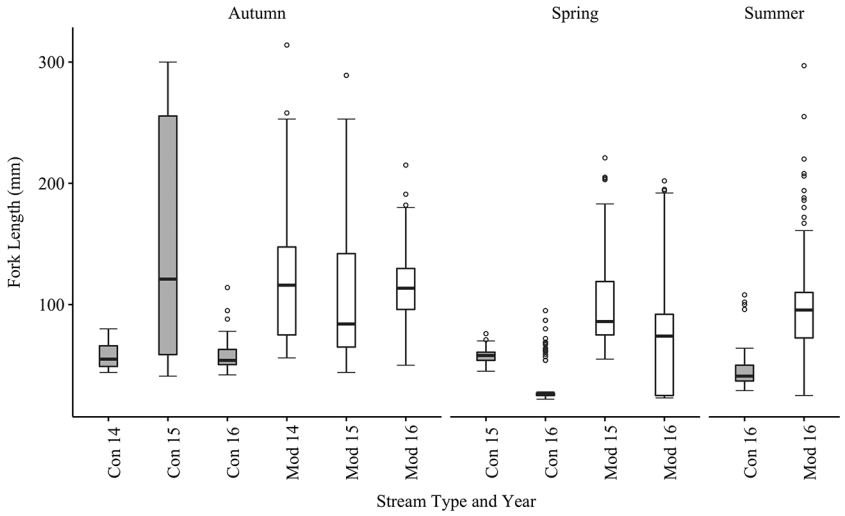


Fig. 6. Differences in mass (g) of (A) post-YOY trout (FL 61–121 mm) and (B) YOY parr (FL 31–60 mm) between the modified and control streams. The box plots illustrate the median (horizontal line), interquartile range (boxes) and overall range up to 1.5 times the interquartile range (whiskers). All outliers are depicted (clear circles).

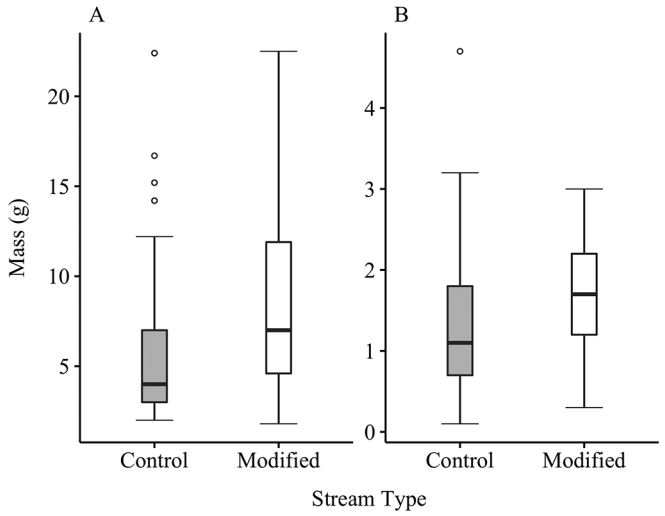
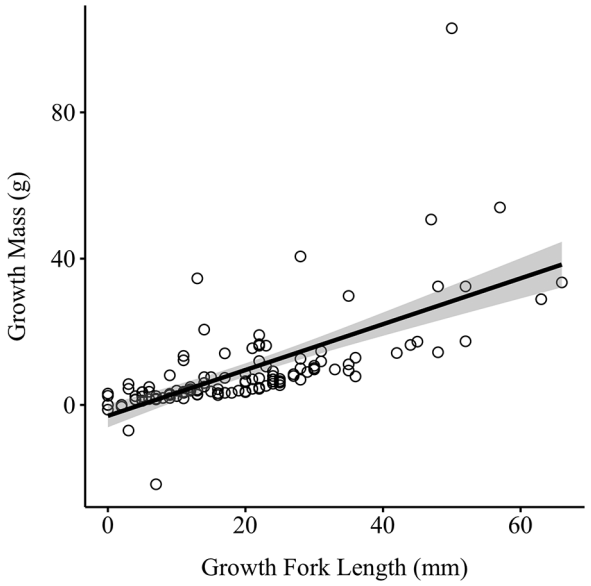


Fig. 7. The linear relationship between growth in mass (g) and FL (mm) of trout captured in the modified stream. Grey shading indicates 95% confidence intervals.



0.05 ± 0.13%·day^{-1}; spring–summer 2015, mean ± SD = 0.56 ± 0.19%·day^{-1}; winter 2015–2016, mean ± SD = 0.30 ± 0.13%·day^{-1}; spring 2016, mean ± SD = 0.72 ± 0.33%·day^{-1}; summer 2016, mean ± SD = 0.30 ± 0.21%·day^{-1}), with the highest during the spring and the lowest during the winter. During both winter sampling periods some trout demonstrated growth in mass (g) that exceeded that predicted by the optimum growth model (Fig. 8).

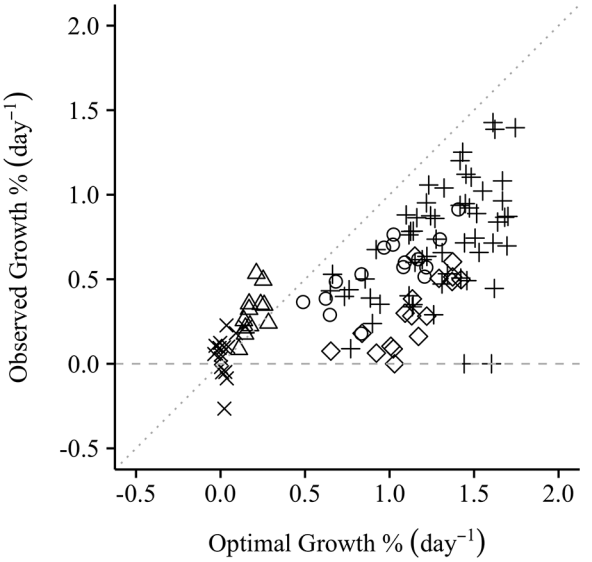
Invertebrate abundance

In support of H5, mean invertebrate abundance was greater in the modified (mean ± SD = 52.91 ± 51.80) than the control stream (mean ± SD = 14.434 ± 7.50) ($t_{22.9}$ = 3.5258, p = 0.002, d = 1.04). NMDS ordination revealed that invertebrate community structures in the modified stream were separated in community ordination on 2-axes from those in the control stream (Adonis $F_{[1,44]}$ = 15.24, $p < 0.001$, R^2 = 0.26, stress = 0.149) (Fig. 9). Chironomidae (–0.906), Sphaeriidae (–0.964), Glossiphoniidae (–1.23), Sialidae (–0.923), Physidae (–0.971) and Dytiscidae (–0.834) were most associated with the beaver-modified stream while Philopotamidae (0.903), Thaumaleidae (1.204), Capniidae (0.859), Simuliidae (0.911), Planorbidae (0.760) and Perlodidae (0.69) were most associated with the control stream.

Discussion

This study represents the first investigation into the response of a population of brown trout to modifications of the fluvial landscape by re-established Eurasian beavers in Great Britain. The presence of a series of dams in a beaver-modified stream resulted in the creation of impounded reaches that were deeper, wider and slower flowing than a nearby unmodified (control)

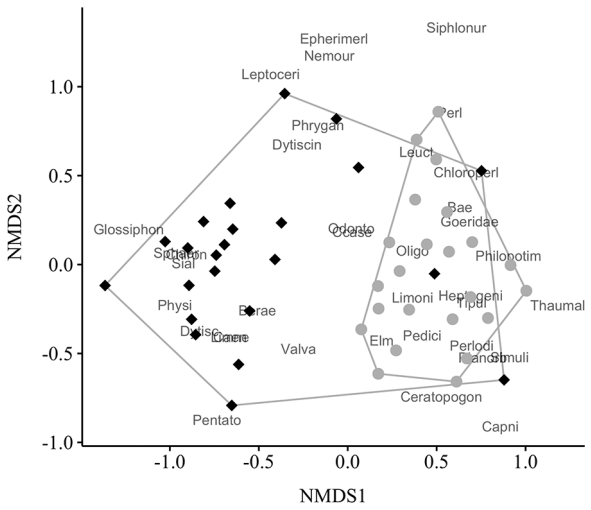
Fig. 8. Relationship between observed seasonal growth rates of brown trout inhabiting a beaver-modified stream and that predicted by an optimal growth model that assumes fish are fed to satiation under laboratory conditions (Elliott et al. 1995): times symbols — winter 2014–2015 (October–December 2014 – March–April 2015 [n = 16]), circles — spring–summer 2015 (March–April 2015 – October 2015 [n = 16]), triangles — winter 2015–2016 (October 2015 – April–May 2016 [n = 12], plus symbols — spring 2016 (April–May 2016 – July 2016 [n = 58]), diamonds — summer 2016 (July–October 2016 [n = 17]).



stream. As predicted, trout were more abundant (when YOY fish were excluded), larger, and had access to a greater abundance of invertebrate food in the beaver-modified stream. Although trout abundance was higher, there was no difference in density due to the larger surface areas associated with the beaver impounded reaches. Furthermore, trout in the modified stream exhibited a wider range of size classes and positive growth throughout the year, which in the winter was higher than that predicted by an optimal growth model for some individuals.

The observation that YOY trout were more abundant and densely distributed in the shallow control than the beaver-modified stream, particularly during spring and summer, reflects the importance of this habitat for spawning. Prior to the introduction of beaver, both streams that entered into the loch had similar geomorphological and hydrological characteristics. The impoundment of sections of the modified stream due to the construction of a series of dams would likely have reduced the availability of suitable trout spawning habitat (Armstrong et al. 2003) due to the increase in depth, reduction in flow velocity, and deposition of fine sediments. Furthermore, the dams themselves may have directly impeded the spawning movements of adult trout, particularly during periods of low flow (Kemp et al. 2012). As such, the relative importance of the control stream as a spawning site for adult trout migrating from the loch would have increased with the beaver modification of the neighbouring tributary. Indeed, this was indicated by the large number of mature (≥150 mm) fish captured in the control during the autumn 2015 survey followed by a higher abundance of the youngest age class, compared to the modified stream, during the following spring and summer. As the two habitats are connected through the linkage to the loch, and greater abundance of older age classes (1+) were observed in the modified reaches alongside declines in abundance of YOY fish in the control stream by the autumn, it is likely that growing fish either redistributed to habitats more

Fig. 9. Nonmetric multidimensional scaling (NMDS) ordination plot of invertebrate community composition between a beaver-modified stream (black diamonds with polygon) and control stream (grey circles with polygon) in northern Scotland.



conducive to rearing, perhaps as a result of self-thinning (Armstrong 1997) or were lost from the system due to predation. Of seven recaptured trout tagged in the control as parr, one was recaptured in the modified stream, indicating their potential to successfully migrate between streams and pass beaver dams during summer months. No tagged trout from the modified stream were recaptured in the control stream during the study.

The greater wetted width of the modified stream meant that, although larger trout were more abundant, density was no greater than for the control. In other regions where the redistribution of stream-dwelling salmonids has been investigated within streams, a higher abundance and density of fish have been associated with reaches modified by beaver, particularly during the winter months when the deeper ponds provide refuge from adverse conditions (e.g., for North America: Chisholm (1987) for bull trout, *Salvelinus confluentus*; Nickelson et al. (1992) for coho salmon, *Oncorhynchus kisutch*). For example, in the Rocky Mountain streams of Montana (USA), the densities of bull and cutthroat trout (*Oncorhynchus clarkii*) are lower when temperatures drop below 7 °C in all habitats, except beaver ponds (Cunjak 1996) where both species overwinter in large aggregations (Jakober et al. 1998). Conversely, the densities of fry in our study were higher in the control than the modified stream, particularly during the spring and summer. This indicates the importance and suitability of this habitat, dominated by pebble substrate, for spawning. The control stream, however, provided insufficient suitable habitat to maintain larger numbers of older trout. As a result, seasonal shifts in habitat availability (e.g., associated with drought or freeze-up), along with predation (Cunningham et al. 2002 for Scottish streams; Heggenes and Borgstrøm 1988 for Norwegian streams; R. Needham, personal observation) and self-thinning if at carrying capacity (Armstrong et al. 2003; Milner et al. 2003), likely explains the reduction in density in the control stream as fish moved to the loch and the beaver-modified stream.

Beaver-modified reaches supported a wider range of trout size classes than the control stream, reflecting the relationship between habitat heterogeneity and the availability of suitable habitat for multiple life stages. In particular, trout in the modified reaches tended to be characteristically larger than those in the control stream. This supports the findings of several other researchers in relation to both the North American (Malison et al. 2015) and European (Hägglund and Sjöberg 1999) context,

and the general "rule-of-thumb" that larger trout tend to occupy deeper pool habitats when available (Armstrong et al. 2003). There are a number of logical explanations for this, not least that deeper habitat provides greater protection for larger trout from native piscivorous predators such as Eurasian otter (*Lutra lutra*) and heron (*Ardea cinerea*) (as well as the introduced North American mink, *Mustela vison*) (Rosenfeld and Boss 2001; White and Rahel 2008), especially when reinforced by the shelter provided by woody structures common in beaver ponds, thus enabling fish more time to forage (Sigourney et al. 2006). Furthermore, beaver pools also provide refuge from adverse flow (Hutchings 1986; Sigourney et al. 2006) or freeze-up (Jakober et al. (1998); Lindstrom and Hubert (2004) for North American streams), while at the same time proving to be energetically advantageous if the availability of food is uncompromised (Sigourney et al. 2006), enabling trout to favourably shift their energy input: output ratio. In fact, there is evidence that, compared to unimpounded reaches, invertebrate abundance associated with beaver ponds (e.g., McDowell and Naiman (1986) for Canadian streams) and the dams themselves (e.g., Rolauffs et al. (2001) for German streams) can be substantially higher, as was observed in this study, thus supporting greater abundance and more rapid growth in these environments. This study found that Chironomids were strongly associated with the beaver-modified habitat in comparison to the control stream and were present in much greater abundance. Kelly-Quinn and Bracken (1990) describe larval and adult Chironomids as one of the most frequently consumed prey items for brown trout in Irish streams, while Bridcut (2000) suggest that Dipteran larvae and adults (mostly represented by Chironomidae and Simuliidae) are prey items of high importance to salmonids in the Nethy River, Scotland. This suggests that the beaver ponds support a high abundance of important prey resources for brown trout. Growth rates might be further enhanced if, as was the case in this study, overall densities relative to surface area remain relatively low, leading to reduced competition (e.g., Sigourney et al. (2006) for Atlantic salmon in beaver ponds).

Trout in the beaver-modified reaches exhibited positive growth in all seasons, including the two winter periods. This supports evidence supplied by others that beaver ponds provide suitable habitat that can enhance individual fitness, demonstrated through positive growth (e.g., Sigourney et al. (2006) for juvenile Atlantic salmon parr in Canadian streams; Malison et al. (2015) for juvenile chinook and coho salmon in Alaskan streams; Murphy et al. (1989) for juvenile sockeye salmon (*Oncorhynchus nerka*) in Alaskan streams). Our observation that the growth of some trout during winter was higher than that predicted by an optimal growth model developed for fish fed to satiation under experimental conditions (Elliott et al. 1995) was surprising. It was not possible to measure water temperatures at a sufficiently fine spatial resolution to accurately determine the exact regime experienced by individual fish, instead basing our estimates on coarse-scale temperature logger data for the stream as a whole. It is recognised that Scottish upland streams can experience thermal heterogeneity as a result of interactions between ground, hyporheic, and surface flow (e.g., Malcolm et al. 2002), while beaver ponds are known to have more stable diel temperature regimes during the winter than non-impounded reaches. It is possible that some trout utilised higher temperature microhabitats than expected based on mesoscale measures of temperature during the winter, explaining the more rapid than predicted growth rates. Alternatively, the exploitation of more energy rich food if available in the beaver ponds compared to that used in the laboratory by Elliott (1994), and on which the model was based, may provide another explanation. In this study, the beaver ponds maintained large shoals of stickleback, a species the trout were known to prey on based on observations of stomach contents (R. Needham, personal observation). Furthermore, other studies of wild brown trout populations (e.g., Jensen (1990); Jensen et al. (2000) for Norway; Lobón-Cerviá and Rincón (1998) for Spain; Allen (1985) for New Zealand) also observed growth rates higher than that predicted by the Elliott et al. (1995) model, suggesting that the possibility for genetic variation and local adaptation to drive higher than expected growth should not be discounted.

This study provides evidence that local-scale modification of river habitat by Eurasian beavers can benefit brown trout populations by enhancing the heterogeneity and suitability of habitat for a range of life stages, thus improving abundance and growth, a useful proxy for fitness. Based on previous reviews on the subject (e.g., Kemp et al. 2012), this finding is not unexpected, although it does provide useful confirmation that relationships observed elsewhere appear to hold true for upland areas of northern and western Great Britain. The results may provide helpful information to riparian landowners and policy makers in relation to the management of expanding Eurasian beaver populations in European rivers which host commercially important and sensitive salmonid populations. These findings may go some way to reassure representatives of fisheries interests that, from the perspective of brown trout habitat suitability at least, the presence of beaver may provide a cost-effective and self-sustaining means to maintain and restore the ecological status of upland rivers without threatening native fish populations. Nevertheless, there remains a need to further explore the impact of beaver activity at a catchment scale, and the impact of dams on the movement of multiple species of fish, including the migratory salmonid life stages.

Competing interests

The authors declare there are no competing interests.

Data availability

All data supporting this article are openly available from the University of Southampton repository at https://doi.org/10.5258/SOTON/D1814.

Acknowledgements

We thank the Swift family for access to the field site and accommodation during survey work, and ICER staff, Rob Branch and Fred Swift for their assistance with field work and data collection. The Ph.D. was funded by the NERC Doctoral Training Partnership (SPITFIRE) based at the University of Southampton. Additional funding was provided by the Game and Wildlife Conservation Trust, Trout and Salmon Association and NatureScot. We thank the associated editor and two anonymous reviewers for comments on an earlier version of this manuscript.

References

Acreman, M.C., and Ferguson, A.J.D. 2010. Environmental flows and the European Water Framework Directive. Freshwater Biol. **55**: 32–48. doi:10.1111/j.1365-2427.2009.02181.x.

Allen, K.R. 1985. Comparison of the growth rate of brown trout (*Salmo trutta*) in a New Zealand stream with experimental fish in Britain. J. Anim. Ecol. **54**(2): 487–495. doi:10.2307/4493.

Armstrong, J.D. 1997. Self-thinning in juvenile sea trout and other salmonid fishes revisited. J. Anim. Ecol. **66**(4): 519–526. doi:10.2307/5946.

Armstrong, J.D., Kemp, P.S., Kennedy, G.J.A., Ladle, M., and Milner, N.J. 2003. Habitat requirements of Atlantic salmon and brown trout in rivers and streams. Fish. Res. **62**: 143–170. doi:10.1016/S0165-7836(02)00160-1.

Belletti, B., de Leaniz, C.G., Jones, J., Bizzi, S., Börger, L., Segura, G., et al. 2020. More than one million barriers fragment Europe's rivers. Nature, **588**: 436–441. doi:10.1038/s41586-020-3005-2. PMID:33328667.

Bernhardt, E.S., and Palmer, M.A. 2011. River restoration: the fuzzy logic of repairing reaches to reverse catchment scale degradation. Ecol. Appl. **21**: 1926–1931. doi:10.1890/10-1574.1. PMID:21939034.

Best, J. 2019. Anthropogenic stresses on the world's big rivers. Nat. Geosci. **12**: 7–21. doi:10.1038/s41561-018-0262-x.

Bouwes, N., Weber, N., Jordan, C.E., Saunders, W.C., and Tattam, I.A. 2016. Ecosystem experiment reveals benefits of natural and simulated beaver dams to a threatened population of steelhead (*Oncorhynchus mykiss*). Sci. Rep. **6**: 28581. doi:10.1038/srep28581. PMID:27373190.

Bridcut, E.E. 2000. A study of terrestrial and aerial macroinvertebrates on river banks and their contribution to drifting fauna and salmonid diets in a Scottish catchment. Hydrobiologia, **427**: 83–100. doi:10.1023/A:1003927331472.

Brown, A.G., Lespez, L., Sear, D.A., Macaire, J.-J., Houben, P., Klimek, K., et al. 2018. Natural vs anthropogenic streams in Europe: history, ecology and implications for restoration, river-rewilding and riverine ecosystem services. Earth Sci. Rev. **180**: 185–205. doi:10.1016/j.earscirev.2018.02.001.

BSWG. 2015. Final report of the Beaver Salmonid Working Group (prepared for The National Species Reintroduction Forum, Inverness). Available from https://www.nature.scot/beaver-salmonid-working-group-final-report-2015.

Burchsted, D., Daniels, M., and Wohl, E. 2014. Introduction to the special issue on discontinuity of fluvial systems. Geomorphology, **205**: 1–4. doi:10.1016/j.geomorph.2013.04.004.

Campbell-Palmer, R., Schwab, G., Girling, S., Lisle, S., and Gow, D. 2015. Managing wild Eurasian beavers: a review of European management practices with consideration for Scottish application. Commissioned Report No. 812. NatureScot, Iverness, UK.

Chisholm, I.M., Hubert, W.A., and Wesche, T.A. 1987. Winter stream conditions and use of habitat by brook trout in high-elevation Wyoming streams. Trans. Am. Fish. Soc. **116**(2): 176–184. doi:10.1577/1548-8659(1987)116<176:WSCAUO>2.0.CO;2.

Collen, P., and Gibson, R. 2000. The general ecology of beavers (*Castor* spp.), as related to their influence on stream ecosystems and riparian habitats, and the subsequent effects on fish — a review. Rev. Fish Biol. Fish. **10**: 439–461. doi:10.1023/A:1012262217012.

Cunjak, R.A. 1996. Winter habitat of selected stream fishes and potential impacts from land use activity. Can. J. Fish. Aquat. Sci. **53**(S1): 267–282. doi:10.1139/f95-275.

Cunningham, P.D., Brown, L.J., and Harwood, A.J. 2002. Predation and scavenging of salmon carcasses along spawning streams in the Scottish Highlands. Final report for the Atlantic Salmon Trust. Wester Ross Fisheries Trust, Wester Ross, UK.

Darwall, W.R.T., Holland, R.A., Smith, K.G., Allen, D., Brooks, E.G.E., Katarya, V., et al. 2011. Implications of bias in conservation research and investment for freshwater species. Conserv. Lett. **4**: 474–482. doi:10.1111/j.1755-263X.2011.00202.x.

Elliott, J.M. 1994. Quantitative ecology and the brown trout. Oxford Series in Ecology and Evolution. Oxford University Press, Oxford, UK.

Elliott, J.M., Hurley, M.A., and Fryer, R.J. 1995. A new, improved growth model for brown trout, *Salmo trutta*. Funct. Ecol. **9**: 290–298. doi:10.2307/2390576.

European Union. 2000. Directive of the European parliament and of the council 2000/60/EC establishing a framework for community action in the field of water policy. Official Journal of the European Union, **L 327**: 1–71.

Hägglund, Å., and Sjöberg, G. 1999. Effects of beaver dams on the fish fauna of forest streams. For. Ecol. Manage. **115**: 259–266. doi:10.1016/S0378-1127(98)00404-6.

Halley, D.J., and Rosell, F. 2002. The beaver's reconquest of Eurasia: status, population development and management of a conservation success. Mammal Rev. **32**(3): 153–178. doi:10.1046/j.1365-2907.2002.00106.x.

Heggenes, J., and Borgstrøm, R. 1988. Effect of mink, *Mustela vison* Schreber, predation on cohorts of juvenile Atlantic salmon, *Salmo salar* L., and brown trout, *S. trutta* L., in three small streams. J. Fish Biol. **33**(6): 885–894. doi:10.1111/j.1095-8649.1988.tb05536.x.

Hutchings, J.A. 1986. Lakeward migration by juvenile Atlantic salmon, *Salmo salar*. Can. J. Fish. Aquat. Sci. **43**(4): 732–741. doi:10.1139/f86-090.

Jaccard, J. 1998. Interaction effects in factorial analysis of variance. Sage University Papers Series on Quantitative Applications in the Social Sciences (Series No. 07-118). SAGE, Thousand Oaks, Calif.

Jakober, M.J., McMahon, T.E., Thurow, R.F., and Clancy, C.G. 1998. Role of stream ice on fall and winter movements and habitat use by bull trout and cutthroat trout in Montana headwater streams. Trans. Am. Fish. Soc. **127**: 223–235. doi:10.1577/1548-8659(1998)127<0223:ROSIOF>2.0.CO;2.

Jensen, A.J. 1990. Growth of young migratory brown trout *Salmo trutta* correlated with water temperature in Norwegian rivers. J. Anim. Ecol. **59**: 603–614. doi:10.2307/4883.

Jensen, A.J., Forseth, T., and Johnsen, B.O. 2000. Latitudinal variation in growth of young brown trout *Salmo trutta*. J. Anim. Ecol. **69**: 1010–1020. doi:10.1046/j.1365-2656.2000.00457.x.

Johnson, S.L., Rahel, F.J., and Hubert, W.A. 1992. Factors influencing the size structure of brook trout populations in beaver ponds in Wyoming. N. Am. J. Fish. Manage. **12**(1): 118–124. doi:10.1577/1548-8675(1992)012<0118:FITSSO>2.3.CO;2.

Jones, C.G., Lawton, J.K., and Shachak, M. 1994. Organisms as ecosystem engineers. Oikos, **69**(3): 373–386. doi:10.2307/3545850.

Jones, C.G., Lawton, J.K., and Shachak, M. 1997. Positive and negative effects of organisms as physical ecosystem engineers. Ecology, **78**(7): 1946–1957. doi:10.1890/0012-9658(1997)078[1946:PANEOO]2.0.CO;2.

Kelly-Quinn, M., and Bracken, J.J. 1990. A seasonal analysis of the diet and feeding dynamics of brown trout, *Salmo trutta* L., in a small nursery stream. Aquacult. Res. **21**: 107–124. doi:10.1111/j.1365-2109.1990.tb00386.x.

Kemp, P.S., Worthington, T.A., Langford, T.E.L., Tree, A.R.J., and Gaywood, M.J. 2012. Qualitative effects of reintroduced beavers on stream fish. Fish Fish. **13**: 158–181. doi:10.1111/j.1467-2979.2011.00421.x.

Knudsen, G.J. 1962. Relationship of beaver to forests, trout and wildlife in Wisconsin. Technical Bulletin 25. Wisconsin Department Natural Resources, Madison, Wisc. pp. 1–52.

Lindstrom, J.W., and Hubert, W.A. 2004. Ice processes affect habitat use and movements of adult cutthroat trout and brook trout in a Wyoming foothills stream. N. Am. J. Fish. Manage. **24**: 1341–1352. doi:10.1577/M03-223.1.

Lobón-Cerviá, J., and Rincón, P.A. 1998. Field assessment of the influence of temperature on growth rate in a brown trout population. Trans. Am. Fish. Soc. **127**: 718–728. doi:10.1577/1548-8659(1998)127<0718:FAOTIO>2.0.CO;2.

Lokteff, R.L., Roper, B.B., and Wheaton, J.M. 2013. Do beaver dams impede the movement of trout? Trans. Am. Fish. Soc. **142**: 1114–1125. doi:10.1080/00028487.2013.797497.

Malcolm, I.A., Soulsby, C., and Youngson, A.F. 2002. Thermal regime in the hyporheic zone of two contrasting salmonid spawning streams: ecological and hydrological implications. Fish. Manage. Ecol. **9**: 1–10. doi:10.1046/j.1365-2400.2002.00276.x.

Malison, R.L., and Halley, D.J. 2020. Ecology and movement of juvenile salmonids in beaver-influenced and beaver-free tributaries in the Trøndelag province of Norway. Ecol. Freshwater Fish. **29**(4): 623–639. doi:10.1111/eff.12539.

Malison, R.L., Eby, L., and Stanford, J.A. 2015. Juvenile salmonid growth, survival and production in a large river floodplain modified by beavers (*Castor canadensis*). Can. J. Fish. Aquat. Sci. **72**(11): 1639–1652. doi:10.1139/cjfas-2015-0147.

McDowell, D.M., and Naiman, R.J. 1986. Structure and function of a benthic invertebrate stream community as influenced by beaver (*Castor canadensis*). Oecologia, **68**(4): 481–489. doi:10.1007/BF00378759. PMID:28311700.

Milner, N.J., Elliott, J.M., Armstrong, J.D., Gardiner, R., Welton, J.S., and Ladle, M. 2003. The natural control of salmon and trout populations in streams. Fish. Res. **62**: 111–125. doi:10.1016/S0165-7836(02)00157-1.

Mitchell, S.M., and Cunjak, R.A. 2007. Stream flow, salmon and beaver dams: roles in the structuring of stream fish communities within an anadromous salmon dominated stream. J. Anim. Ecol. **76**: 1062–1074. doi:10.1111/j.1365-2656.2007.01286.x. PMID:17922703.

Moss, B. 2008. Water pollution by agriculture. Philos. Trans. R Soc. Lond. B Biol. Sci. **363**: 659–666. doi:10.1098/rstb.2007.2176. PMID:17666391.

Mossa, J., Chen, Y.-H., Kondolf, G.M., and Walls, S.P. 2020. Channel and vegetation recovery from dredging of a large river in the Gulf coastal plain, USA. Earth Surf. Processes Landforms, **45**: 1926–1944. doi:10.1002/esp.4856.

Müller-Schwarze, D. 2011. The beaver: its life and impacts. 2nd ed. Cornell University, Ithaca, New York.

Murphy, M.L., Heifetz, J., Thedinga, J.F., Johnson, S.W., and Koski, K.V. 1989. Habitat utilization by juvenile Pacific salmon (*Onchorynchus*) in the Glacial Taku River, Southeast Alaska. Can. J. Fish. Aquat. Sci. **46**(10): 1677–1685. doi:10.1139/f89-213.

Naimen, R.J., Johnston, C.A., and Kelley, J.C. 1988. Alteration of North American streams by beaver: the structure and dynamics of streams are changing as beaver recolonize their historic habitat. BioScience, **38**(11): 753–762. doi:10.2307/1310784.

Nickelson, T.E., Rodgers, J.D., Johnson, S.L., and Solazzi, M.F. 1992. Seasonal changes in habitat use by juvenile coho salmon (*Oncorhynchus kisutch*) in Oregon coastal streams. Can. J. Fish. Aquat. Sci. **49**(4): 783–789. doi:10.1139/f92-088.

Pollock, M.M., Heim, M., and Werner, D. 2003. Hydrologic and geomorphic effects of beaver dams and their influence on fishes. *In* The Ecology and Management of Wood in World Rivers. *Edited by* S.V. Gregory, K. Boyer, and A. Gurnell. Symposium 37. American Fisheries Society, Bethesda, Md. pp. 213–233. doi:10.47886/9781888569568.ch11.

Pollock, M.M., Pess, G.R., Beechie, T.J., and Montgomery, D.R. 2004. The importance of beaver ponds to coho salmon production in the Stillaguamish River Basin, Washington, USA. N. Am. J. Fish. Manage. **24**: 749–760. doi:10.1577/M03-156.1.

Pollock, M.M., Beechie, T.J., Wheaton, J.M., Jordan, C.E., Bouwes, N., Weber, N., and Volk, C. 2014. Using beaver dams to restore incised stream ecosystems. Bioscience, **64**: 279–290. doi:10.1093/biosci/biu036.

Puttock, A., Graham, H., Carless, D., and Brazier, R.E. 2018. Sediment and nutrient storage in a beaver engineered wetland. Earth Surf. Processes Landforms, **43**: 2358–2370. doi:10.1002/esp.4398.

Rabe, F.W. 1970. Brook trout populations in Colorado beaver ponds. Hydrobiologia, **35**: 431–448. doi:10.1007/BF00184569.

Reid, G.M., Contreras MacBeath, T., and Csatádi, K. 2013. Global challenges in freshwater-fish conservation related to public aquariums and the aquarium industry. Int. Zoo Yearb. **47**: 6–45. doi:10.1111/izy.12020.

Rolauffs, P., Hering, D., and Lohse, S. 2001. Composition, invertebrate community and productivity of a beaver dam in comparison to other stream habitat types. Hydrobiologia, **459**(1): 201–212. doi:10.1023/A:1012507613952.

Rosenfeld, J.S., and Boss, S. 2001. Fitness consequences of habitat use for juvenile cutthroat trout: energetic costs and benefits in pools and riffles. Can. J. Fish. Aquat. Sci. **58**(3): 585–593. doi:10.1139/f01-019.

Rotiroti, M., Bonomi, T., Sacchi, E., McArthur, J.M., Stefania, G.A., Zanotti, C., et al. 2019. The effects of irrigation on groundwater quality and quantity in a human-modified hydro-system: the Oglio River basin, Po Plain, northern

Italy. Sci. Total Environ. **672**: 342–356. doi:10.1016/j.scitotenv.2019.03.427. PMID:30959301.
Rupp, R. 1955. Beaver-trout relationship in the headwaters of Sunkhaze Stream, Maine. Trans. Am. Fish. Soc. **84**(1): 75–85. doi:10.1577/1548-8659(1954)84[75:BRITHO]2.0.CO;2.
SFCC. 2014. Scottish Fisheries Co-ordination Centre (SFCC) training manual. Available from https://sfcc.co.uk/assets/files/SFCC%20Electrofishing%20Team%20Leader%20Manual_2014%282%29.pdf.
Sigourney, D.B., Letcher, B.H., and Cunjak, R.A. 2006. Influence of beaver activity on summer growth and condition of age-2 Atlantic salmon parr. Trans. Am. Fish. Soc. **135**: 1068–1075. doi:10.1577/T05-159.1.
Smith, J.M., and Mather, M.E. 2013. Beaver dams maintain fish biodiversity by increasing habitat heterogeneity throughout a low-gradient stream network. Freshwater Biol. **58**: 1523–1538. doi:10.1111/fwb.12153.
Taylor, B.R., Macinnis, C., and Floyd, T.A. 2010. Influence of rainfall and beaver dams on upstream movement of spawning Atlantic salmon in a restored brook in Nova Scotia, Canada. River Res. Appl. **26**: 183–193. doi:10.1002/rra.1252.
Theodoropoulos, C., Stamou, A., Vardakas, L., Papadaki, C., Dimitriou, E., Skoulikidis, N., and Kalogianni, E. 2020. River restoration is prone to failure unless pre-optimized within a mechanistic ecological framework | Insights from a model-based case study. Water Res. **173**: 115550. doi:10.1016/j.watres.2020.115550. PMID:32035279.
White, S.M., and Rahel, F.J. 2008. Complementation of habitats for Bonneville cutthroat trout in watersheds influenced by beavers, livestock, and drought. Trans. Am. Fish. Soc. **137**(3): 881–894. doi:10.1577/T06-207.1.
Wohl, E., Angermeier, P.L., Bledsoe, B., Kondolf, G.M., MacDonnell, L., Merritt, D.M., et al. 2005. River restoration. Water Resour. Res. **41**: W10301. doi:10.1029/2005WR003985.
Wright, J.P., Jones, C.G., and Flecker, A.S. 2002. An ecosystem engineer, the beaver, increases species richness at the landscape scale. Oecologia, **132**: 96–101. doi:10.1007/s00442-002-0929-1. PMID:28547281.
Zajicek, P., and Wolter, C. 2019. The effects of recreational and commercial navigation on fish assemblages in large rivers. Sci. Total Environ. **646**: 1304–1314. doi:10.1016/j.scitotenv.2018.07.403. PMID:30235616.

Appendix A

Table A1. Physical habitat characteristics of an unmodified (control) and beaver-modified stream.

Location	Length (m)	Mean wetted width (m)	Mean bank width (m)	Area (m^2)	Depth (m)	Flow type	Velocity readings (m^{-s}) (±SD)	Substrate composition
Control Reach 1	40	0.52	0.45	20.75	<0.1	RI (100%)		Pebble (60%)
Riffle							0.23±0.005	Gravel (20%)
Pool							—	Sand (20%)
Control Reach 2	26	0.65	0.53	16.87	<0.1	RI (100%)		Pebble (60%)
Riffle							0.38±0.005	Gravel (20%)
Pool							—	Sand (20%)
Control Reach 3	42	1.00	0.96	42.17	≤0.2	RI (70%), SP (30%)		Pebble (30%)
Riffle							0.335±0.033	Cobble (30%)
Pool							0.132±0.005	Gravel (20%)
								Sand (20%)
Control Reach 4	30	1.03	1.10	30.83	≤0.2	SP (70%), RI (30%)		Cobble (30%)
Riffle							0.372±0.009	Boulder (30%)
Pool							0.120±0.007	Pebble (20%)
								Gravel (10%)
								Sand (10%)
Modified Reach 1	50	4.20	4.95	215.53	>0.5	DP (90%), SP (10%)		Silt (90%)
Pool							0.022±0.003	Gravel (5%)
Pool							0.028±0.004	Pebble (5%)
Modified Reach 2	44	6.02	6.85	261.77	>0.5	DP (95%), RI (5%)		Silt (95%)
Riffle							0.040±0.003	Gravel (5%)
Pool							0.041±0.002	
Dam 3 Bypass Channel	30	0.78	0.87	37.60	≤0.2	SP (70%), RI (30%)		Silt (70%)
Riffle							0.214±0.019	Gravel (15%)
Pool							0.204±0.005	Sand (15%)
Modified Reach 3	69	5.76	8.56	613.84	0.3 – >0.5	DP (80%), RI (15%), DG (5%)		Silt (65%)
Pool							0.048±0.003	Gravel (20%)
Pool							0.05±0.003	Sand (10%)
Riffle							1.101±0.005	Pebble (5%)
Pool							0.07±0.002	
Modified Reach 4	44	3.48	3.96	232.34	>0.5	DP (85%), DG (10%), RI (5%)		Silt (65%)
Riffle							0.209±0.006	Gravel (25%)
Pool							0.071±0.003	Sand (10%)
Pool							0.076±0.005	

Note: Flow characteristic abbreviations are listed in order of dominance: SM — still marginal; DP — deep pool; SP — shallow pool; DG — deep glide; SG — shallow glide; RU — run; RI — riffle; and TO — torrent. Flow velocity (0.001 $m{\cdot}s^{-1}$ resolution averaged over 60 s) 0.6 of the total depth, midchannel in the centre of the reach. Where flow types varied within reach one reading was taken in each flow type. Note mean wetted bank width in control reaches 1, 2 and 3 was greater than bank width due to heavily undercut banks.